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PROBLEMS & PARADIGMS

Prospects & Overviews

How to become a crab: Phenotypic constraints on a recurring body plan

Joanna M. Wolfe[1] | Javier Luque[1,2,3] | Heather D. Bracken-Grissom[4]

[1] Museum of Comparative Zoology and Department of Organismic & Evolutionary Biology, Harvard University, Cambridge, Massachusetts, USA

[2] Smithsonian Tropical Research Institute, Balboa–Ancon, Panama

[3] Department of Earth and Planetary Sciences, Yale University, New Haven, Connecticut, USA

[4] Institute of Environment and Department of Biological Sciences, Florida International University, North Miami, Florida, USA

Correspondence
Joanna M. Wolfe, Museum of Comparative Zoology and Department of Organismic & Evolutionary Biology, Harvard University, 26 Oxford St, Cambridge, MA 02138, USA.
Email: jowolfe@g.harvard.edu

Abstract

A fundamental question in biology is whether phenotypes can be predicted by ecological or genomic rules. At least five cases of convergent evolution of the crab-like body plan (with a wide and flattened shape, and a bent abdomen) are known in decapod crustaceans, and have, for over 140 years, been known as "carcinization." The repeated loss of this body plan has been identified as "decarcinization." In reviewing the field, we offer phylogenetic strategies to include poorly known groups, and direct evidence from fossils, that will resolve the history of crab evolution and the degree of phenotypic variation within crabs. Proposed ecological advantages of the crab body are summarized into a hypothesis of phenotypic integration suggesting correlated evolution of the carapace shape and abdomen. Our premise provides fertile ground for future studies of the genomic and developmental basis, and the predictability, of the crab-like body form.

KEYWORDS
Anomura, Brachyura, carcinization, convergent evolution, Crustacea, morphological integration, phylogeny

INTRODUCTION

Biologists strive to explain the evolution of form, and the drivers of biodiversity across related groups. Instances of convergent evolution are emerging model systems to link such evolutionary patterns and processes, as they provide naturally occurring experimental replicates, including evidence of shared phenotypic constraints. Here, we focus on the success of the crab body plan within the economically and ecologically significant decapod crustaceans, as a system to address these fundamental questions.

Crabs are one of the most iconic groups of invertebrates, as they play an integral role in the aquarium trade, fisheries and aquaculture, and are celebrated through festivals, parades, and social media memes, and as the constellation and astrological sign *Cancer*. The groups we refer to as crabs are members of two decapod crustacean infraorders, together known as Meiura. These comprise Brachyura or "true" crabs (e.g., fiddler crabs, spider and decorator crabs, mud crabs, frog crabs, and swimming crabs), and Anomura or "false" crabs (e.g., porcelain crabs, hermit and king crabs, mole crabs, and squat lobsters). The most visible difference between true and false crabs is the apparent difference in number of walking legs: four and three pairs, respectively (the posterior pair is present but reduced in anomurans, often concealed in the gill chamber). Several other features differentiate anomurans and brachyurans, such as the position of the molting plane of weakness, the length of the antennae (usually longer in anomurans), and the position of antennae with respect to the eyes (one pair to the side of the eyes in anomurans, both pairs of antennae between the eyes in brachyurans).[1,2] The overwhelming majority of extant decapod species (>9500 of ∼15,000) are meiurans.[3] By contrast, the remaining diversity of decapods is distributed into eight other infraorders and one suborder, including lobsters, crayfish, prawns, and shrimp.

Carcinization (a generally wide and flattened shape; Figure 1 and Box 1), or the crab-like body plan, has evolved at least five times, and has been lost at least seven times within meiuran crustaceans
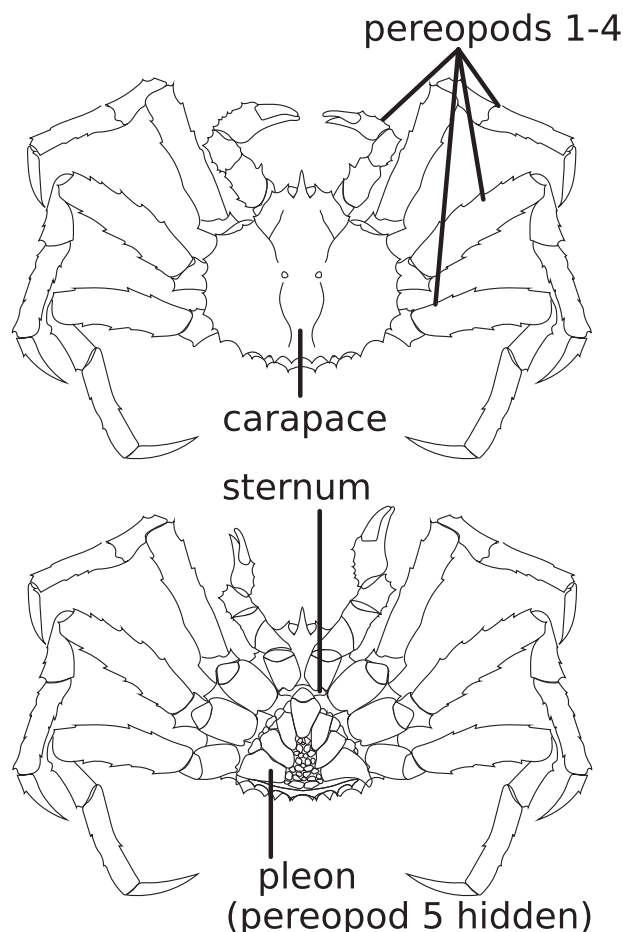
FIGURE 1 Basic anatomical terminology for an exemplar king crab (Lithodoidea: Lithodidae: *Paralithodes camtschaticus*)

(simplified in Figure 2). The reasons for repeated evolution of the crab-like body plan remain a mystery,[4,5] although there seems to be a correlation between body form and ecology,[2] with protective and locomotory behaviors as examples. Carcinized lineages thrive in almost every habitat on Earth, ranging from lively coral reefs to isolated marine caves, from abyssal oceanic plains to mountain streams, from terrestrial to aquatic ecosystems. Morphological disparity across carcinized lineages is equally impressive, with body shapes in endless forms most beautiful, and sizes ranging from millimeters to meters. Given the high morphological variation, species richness, and broad distribution of extant crabs, and their rich fossil record (Figure 3), crabs are an ideal group to study trends in biodiversity through time.

Convergence is common on relatively recent timescales (fewer than ~20 million years), such as in island ecomorphs in anoles[6] and plants,[7] mimicry in butterflies,[8] and microbiota composition in carnivorous plants,[9] among numerous examples. Ancient events (over 540 million years ago) also result in convergence, such as the evolution of metazoan eyes. In the latter cases, the phenotype is usually not replicated as precisely.[10] Meiuran evolution reflects moderate distances between groups, approximately 200–350 million years.[11] As we do not currently know whether parallelism (deep homology,[12] or conservation of pre-existing ancestral genetic regulatory mechanisms)

or "true" convergence (homoplasy, or similar phenotypes arising from completely different ancestors) underpins the crab-like body plan, we use the general term "convergence" to refer to the pattern of repeated evolution of carcinization. The crab system is an emerging example where it is becoming possible to trace the pattern of convergence, infer shared constraints on the body form, and eventually uncover underlying mechanisms and new strategies to predict phenotypic evolution.

CARCINIZATION HAS BEEN GAINED AND LOST THROUGHOUT DECAPOD EVOLUTION

Attempts to infer the convergent pattern of carcinized forms have inspired crustacean researcher for over 140 years.[4,5,13–20] From a hypothesis based on our previous phylogenetic contributions[2,4,11] (Figure 2), evolution of carcinization has fully occurred once or twice in Brachyura (> 7000 species of true crabs), in sponge crabs (Figure 2A) and especially in eubrachyurans (Figures 2E–F, 3J), and at least three times during the evolution of Anomura (>2500 species) in porcelain crabs (Figures 2H, 3B), hairy stone crabs (Figure 2J), and king crabs (Figure 2N).[4,5,13] Carcinization has been lost at least seven times, and likely several other times, among fossil and living meiurans,[2] representing instances of decarcinization, or a dramatic departure from an ancestral crab-like body form. Note that the pattern of carcinization we primarily describe is not the only possible path of character evolution, but will provide a working hypothesis for the purposes of our discussion.

Progress in resolving crab relationships

Most prior phylogenetic studies have focused on the evolutionary pathway and ancestry of king crab carcinization (Figure 2L–N), addressing questions about the evolution "from king [crab] to hermit [crab], or hermit to king"?[4,17,18,20–23] Despite their carcinized appearance (with broad carapaces and reduced, bent pleons), king crabs are anomurans; their affinity is immediately evident from the specialized posteriormost walking leg. Indeed, all recent phylogenetic work suggests king crabs have evolved from a paraphyletic grade of pagurid hermit crabs (Figure 2M).[4,11,20,23,24] Other examples of carcinization, such as porcelain crabs (Figures 2H, 3B) and especially true crabs (Figures 2A–F, 3H–J) have often been excluded from detailed comparative research, though they offer similar insights into dramatic shifts in body morphology.[25,26] Due to the narrow systematic focus of the past, the unparsimonious history of crab body plan evolution must be reconciled.

Numerous topologies have been proposed for the relationships among families within the infraorders Anomura and Brachyura. However, almost half of the branches on the crab tree of life remain dark, the most comprehensive molecular studies including only ~51% of the total extant families and ~2% of the total species.[4,27] Previous studies have included a maximum of nine housekeeping genes, or whole mitogenomes, but are poorly resolved as these data are uninformative for deep branching events.[28–30] Although Sanger sequencing data

Box 1. Carcinization is the evolutionary process leading to the crab-like body form

This form is perceived as a wide, flat oval or hexagonal shape, as opposed to the elongate, cylindrical shape of a lobster or mud shrimp. A major feature of carcinization is thus the flattening and bending of the pleon (abdomen), to fit beneath the carapace. Basic anatomy illustrated in Figure 1. Specific features[13] common to most carcinized groups include:

- A flattened and widened carapace (at least slightly wider than long), often with lateral margins (raised edges of the dorsal carapace)
- Sternites (sclerotized ventral segments) fused to some degree into a single wide plate called the thoracic sternum or plastron
- A flattened and bent "abdomen" or pleon, hidden from dorsal view, partially or completely covering the thoracic sternum
- Loss or significant reduction of the uropods (appendages of the sixth pleonal somite, usually forming a tail fan in other decapods)
- Fusion of pleonal ganglia, reduction of pleonal muscles (documented for representative anomurans and two species of eubrachyuran[13,93,124])

Decarcinization, or the secondary loss of the crab-like body form, has occurred multiple times in both Brachyura and Anomura. The decarcinized form is more cylindrical, but has evolved from a wide oval shaped ancestor,[2,5] as opposed to the ancestrally uncarcinized forms (that never evolved a crab-like form in the time since their common ancestor with mud shrimp). The striking similarity between uncarcinized and decarcinized groups has led to erroneous classification of certain decarcinized brachyurans as uncarcinized anomuran mole crabs[125]; compare Figures 2C and 2K). Common features of decarcinized crabs include:

- An elongated, narrow carapace
- A pleon that is not strongly flattened and/or bent, and is sometimes visible in dorsal view or even elongated
- Legs with modified distal segments

There are varying degrees of carcinization and decarcinization,[2,5] so not all species can be easily labeled as "carcinized," "uncarcinized," or "decarcinized." Some examples include: the coconut crab *Birgus latro* (a semi-carcinized anomuran with a bent pleon but incompletely fused sternites and no lateral margins) and other hermit crabs that have lost or reduced their domiciles; the porcelain crab *Allopetrolisthes spinifrons* (a "hypercarcinized" anomuran with a sexually dimorphic pleon, strongly resembling brachyurans); the homolodromiid and homoloid brachyurans (which have characteristically carcinized pleons but lack wide carapaces and lateral margins; Figure 2B); the thumbnail crab *Thia scutellata* (a somewhat decarcinized eubrachyuran); and the gall-forming cryptochirid crabs (decarcinized brachyurans, but with the female pleon modified as a large brood pouch).[13,14,25,125,126]

exist for Anomura,[4] fossils have not been included in the complimentary morphological matrix (and thus lack any robust systematic framework). Improved phylogenomic data could leverage recent sequencing of 410 exons[11] that represented only 32 species of meiurans. These loci obtained much stronger support at deep nodes than have previous mitogenomic analyses.[11,29,30] Most anomuran nodes were strongly supported, but contradicted previous phylogenies[4] on the position of mole crabs (Figure 2K) and relationships among non-paguroids. Several squat lobster (Figures 2G, I, 3A) and hermit crab (Figures 2L–M, 3C) lineages remain to be sampled. Deep brachyuran nodes were strongly supported,[11] but the relationships between families had variable support depending on the models applied, and several key taxa were not included (such as most podotreme lineages, and freshwater brachyurans).

The podotreme brachyurans (Figures 2A–D, 3E–I; with sexual openings borne on the coxa in females and males) are critical for inferring the polarity and ancestry of carcinization (and decarcinization). As of yet, molecular phylogenetics has been insufficient to resolve the puzzle of podotremes, therefore our depiction of their extant relationships in Figure 2 relies on morphological data. Anatomically, these crabs lie in between Anomura and Eubrachyura, and all current data strongly support a paraphyletic podotreme grade with brachyuran affinity.[31] Analysis of eight Sanger sequenced genes including 58

of ~100 brachyuran families,[27] analyses of mitogenomes,[30,32] and a recent transcriptomic analysis[33] each recovered podotreme paraphyly (the former with weak support). Relationships recovered among podotremes were entirely contradictory between those analyses. Of 11 extant podotreme families, however, over one third lack molecular data: no sequences have been published for Poupiniidae, Lyreididae, and Phyllotymolinidae, and only a single 18S sequence is available for Homolodromiidae. Meanwhile, morphological trees, including fossils, have sampled more extensively from podotreme lineages.[2,31] Thus, a major goal of future research should represent all meiuran families with morphological data, and all extant families with strongly supported phylogenomic data, for a well-resolved total evidence phylogeny.

Novel body plans appear to have evolved in singleton species

Throughout time, there have been numerous meiurans where a single or a very few species have evolved either carcinization from uncarcinized ancestors, or decarcinization from carcinized ancestors. The most significant extant "singleton" is the carcinized anomuran *Lomis hirta* (Figure 2J), forming the monotypic family Lomisidae endemic to
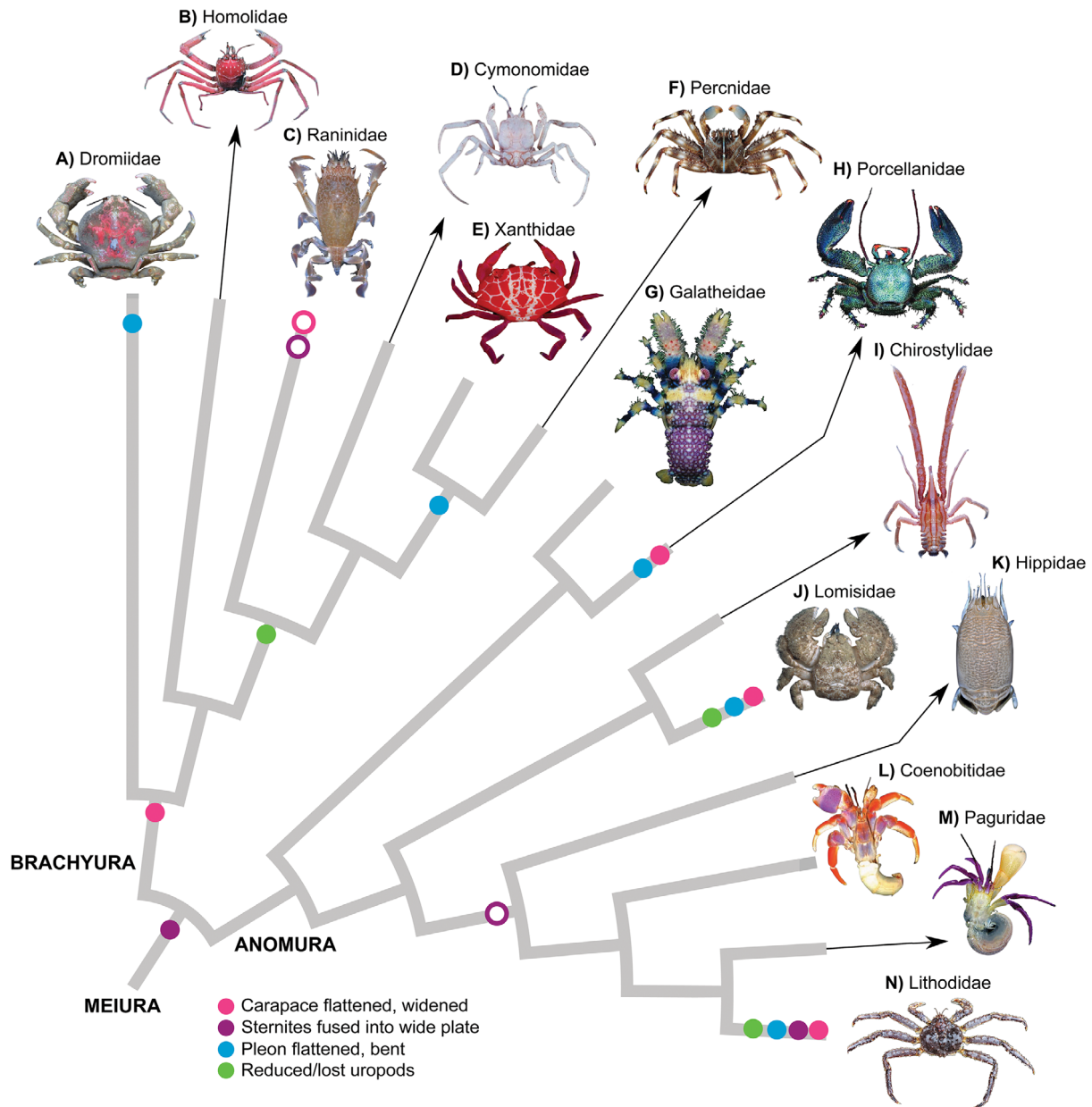
FIGURE 2 Gross morphology in the convergent evolution of representative true crabs (Brachyura), porcelain crabs (Porcellanidae), hairy stone crabs (Lomisidae), and king crabs (Lithodoidea). Losses (open circles) observed in frog crabs (Raninoidea). Topology simplified from [2,4,11]. Body plan features are assumed to be present in the common ancestor of each marked lineage but may vary considerably within each group, see Box 1 for further details. (A) Dromioidea: Dromiidae: *Conchoecetes intermedius* (Phan Thiết, Vietnam). (B) Homoloidea: Homolidae: *Lamoha murotoensis* (Taiwan). (C) Raninoidea: Raninidae: *Raninoides benedicti* (Panama). (D) Cyclodorippoidea: Cymonomidae: *Cymonomus cognatus* (Taiwan). (E) Eubrachyura: Heterotremata: Xanthidae: *Liomera rubra* (Guam). (F) Eubrachyura: Thoracotremata: Percnidae: *Percnon planissimum* (Taiwan). (G) Galathoidea: Galatheidae: *Galathea pilosa* (Mo'orea, French Polynesia). (H) Galatheoidea: Porcellanidae: *Petrolisthes lamarckii* (Taiwan). (I) Chirostyloidea: Chirostylidae: *Uroptychodes grandirostris* (Taiwan). (J) Lomisoidea: Lomisidae: *Lomis hirta* (South Australia). (K) Hippoidea: Hippidae: *Emerita portoricensis* (Rio Grande do Norte, Brazil). (L) Paguroidea: Coenobitidae: *Coenobita clypeatus* (Belize). (M) Paguroidea: Paguridae: *Pylopaguropsis lemaitrei* (Mo'orea, French Polynesia). (N) Lithodoidea: Lithodidae: *Paralithodes camtschaticus* (Narvik, Norway). Photo credits: (A, N) Ondřej Radosta; (B, D, H, I) Tin- Yam Chan; (C, E, G, K, M) Arthur Anker; (F) Ling-Kuang Tseng; (J) Michael Marmach; (L) Darryl Felder

the southern coast of Australia and Tasmania. Over 200 years ago, the species was classified as a member of the carcinized porcelain crabs (Figures 2H, 3B). Further morphological examination suggested membership in the carcinized king crabs (Figure 2N), however, *L. hirta* is now understood as a unique extant lineage.[34,35] Morphological, Sanger,

and mitogenomic data currently suggest this species is related to chirostyloid (Figure 2I) and aeglid squat lobsters,[4,30,36] all of which have uncarcinized forms.

The most significant fossil singleton is the decarcinized brachyuran *Callichimaera perplexa*,[2] a single species described from the Upper
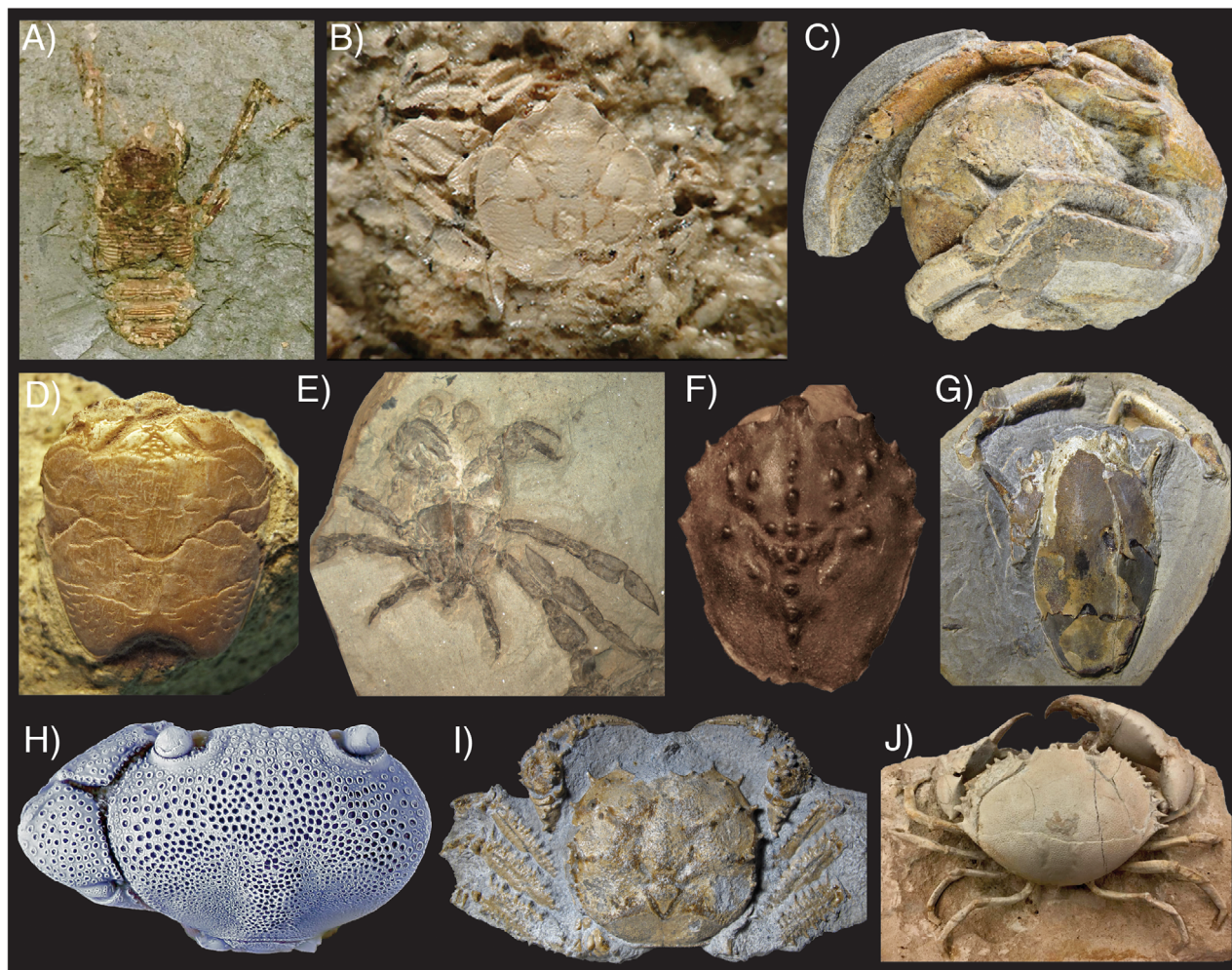
FIGURE 3 Comparison of fossil meiurans representing uncarcinized (A, C, D), carcinized (B, H-J), and decarcinized (E-G) body forms. (A) Anomura: Galatheoidea: galetheoid indet. (Pliocene, Japan). (B) Galatheoidea: Porcellanidae: *Petrolisthes myakkensis* (holotype UF 8678, late Pliocene, Florida, USA). (C) Paguroidea: Diogenidae: *Diogenes augustinus* (holotype MPZ2020/54 articulated without its shell, left lateral view, mid Eocene, Spain). (D) Hippoidea: Albuneidae: *Italialbunea lutetiana* (C-225-1, Eocene, Italy). (E) Brachyura: Callichimaeroidea: Callichimaeridae: *Callichimaera perplexa* (paratype MUN-STRI 27044-02b, Late Cretaceous, Colombia). (F) Palaeocorystoidea: Palaeocorystidae: *Notopocorystes stokesi* (USNM F736, Early Cretaceous, England). (G) Raninoidea: Raninidae: *Raninoides willapensis* (C-064-1, Eocene, USA). (H) Etyoidea: Feldmanniidae: *Caloxanthus americanus* (NPL-62056, Late Cretaceous, USA). (I) Dakoticancroidea: Dakoticancridae: *Avitelmessus grapsoideus* (187-3, Late Cretaceous, USA). (J) Eubrachyura: Heterotremata: Carpilioidea: Zanthopsidae: *Harpactocarcinus punctulatus* (YPM 428818, Eocene, indet). Photo credits: (A) Takashi Ito; (B) from Luque et al.[72] fig. 14A; (C) Fernando Ari-Ferratges; (D, G, I) Àlex Ossó; (E, F, H, J) Javier Luque

Cretaceous with a wide distribution in Colombia and the USA (Figures 3E, 5D). A possible related taxon is the fossil *Retrorsichela laevis*[37] from the Paleocene of New Zealand, which was originally described as a squat lobster. The shape of the fifth and sixth sternites are remarkably similar between *C. perplexa* and *R. laevis*. The claw morphology is also similar, though it is also seen in other un- and decarcinized taxa such as mole crabs (Figures 2K, 3D) and frog crabs (Figures 2C, 3F–G), respectively.[2] Therefore, *R. laevis*, if it is indeed a brachyuran and closely related to *C. perplexa*, could be revised as a decarcinized form as well.

The revelation of *C. perplexa* teases the potential of numerous extinct, but unpreserved, singletons. Return to an ancestral body plan appears to violate Dollo's Law, but such histories have been recorded in taxa that co-opted developmental or genetic mecha-nisms from a common ancestor (as in the simplified case of flower pigmentation[38]). Conversely, new fossil discoveries could refine phylogenetic hypotheses[39] and clades rather than singletons describing a more detailed sequence of evolutionary events, as in the stepwise decarcinization of frog crabs[40] (Figure 3F–G).

IT IS UNCLEAR WHETHER THE EARLIEST CRABS LOOKED LIKE CRABS

Morphologies of fossils close to the divergence time and position of a clade are instrumental to infer whether a trait is ancestrally shared or convergent within the group. Moreover, fossils allow phylogenies to be scaled by time for comparative analyses, and provide Earth history con-
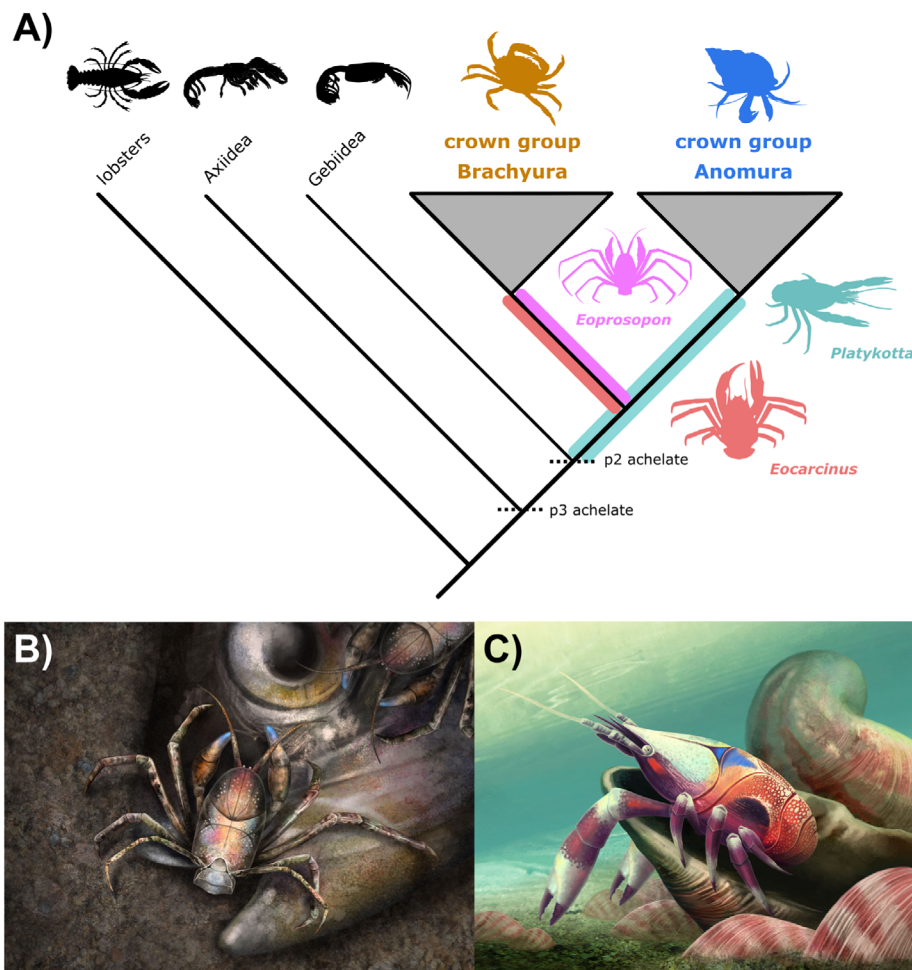
FIGURE 4 Diagnosing the affinities of early stem group crab fossils. (A) Potential positions of early fossils following the favored phylogenomic hypothesis.[11] Abbreviations *p2, p3* refer to the second and third pereopods. Silhouettes from PhyloPic (phylopic.org), with fossils based on recent publications.[46,48,49] (B) Artistic reconstruction of partly carcinized *Eoprosopon klugi* as a facultative scavenger. (C) Artistic reconstruction of uncarcinized *Platykotta akaina* as a dweller of Triassic bivalve reefs. Reconstructions by Franz Anthony

text for evolutionary events.[41–43] From fossil calibrated divergence time estimates, it does not appear that the breadth of crab body plan disparity was achieved early in the evolution of meiurans, due to an early molecular divergence ~350 million years ago, followed by a lag of 100+ million years prior to the respective divergences of crown group anomurans and brachyurans.[4,11,27] Brachyurans in particular have a rich and disparate Late Cretaceous and Cenozoic fossil record (Figure 3E–J), witnessing bouts of morphological experimentation in several Late Cretaceous lineages. The fossil record prior to the Late Cretaceous is considerably more fragmentary (preserving mainly dorsal carapaces), obscuring understanding of early anatomical disparity and therefore the evolution of carcinized and decarcinized forms.[2]

The form of the common ancestor of meiurans and their sister group, the gebiid mud shrimp, may have resembled a mud shrimp itself (a burrower with an elongated carapace and pleon). The ancestral form is inferred from a phylogenetic grade of mud shrimp (axiids and gebiids) relative to meiurans[11], which could equally indicate the mud shrimp forms have evolved independently, however contradictory data are absent. Direct fossil evidence of mud shrimp prior to the Cretaceous

is largely restricted to claw fragments and traces of their burrows.[44] Therefore, we suggest carcinized forms did not evolve in decapods prior to the stem group of meiurans. Unfortunately, the characteristics of the anomuran and brachyuran stem groups are still poorly understood, due to the lack of reliable fossils that can be assigned to either clade with certainty (Figure 4).

There are only three early fossil taxa with sufficiently complete preservation to inform ancestral states. The oldest putative brachyuran fossils are the Early Jurassic *Eocarcinus praecursor*[45] and *Eoprosopon klugi*[46] (Figure 4B). Both of these fossil taxa bear sub-cylindrical carapaces, reminiscent of those in modern homolodromiid crabs (related to the branches of Figure 2A and/or 2B; see [2,47]). Crown group meiurans are united by a lack of chelate second and third pereopods (that is, second and third thoracic legs do not have articulated claws[1,2,48]). In *E. praecursor*, the second and third pereopods are not fully visible, but have recently been reconstructed as distally simple based on multiple specimens.[49] The lack of three-dimensional information about these limbs suggests a crown group meiuran affinity of the species, but cannot reject anomuran affinity.[48,49] Mounting evi-

dence from the combination of total group brachyuran characters, and the lack of characters shared with crown group brachyuran taxa such as dromiaceans and homolids, together suggest that *E. praecursor* is a stem group brachyuran.[49] *E. klugi* exhibits similar character combinations, such as the carapace grooves, claws, and pleonal posture,[46] but it is challenging to discern details as there is only one specimen known. Together, these early fossils suggest the common ancestor of *E. praecursor*, *E. klugi*, and crown group brachyurans was not fully carcinized, possibly with a relatively wide carapace, a partially bent pleon, and may have lost uropods. It is possible that crab-like forms could have appeared multiple times, and to different degrees, within brachyurans (with Figure 2 as one hypothesis).

The oldest putative anomuran is *Platykotta akaina*[50] from the Late Triassic (Figure 4C). This lobster-looking and uncarcinized decapod shares features in common with some anomurans, and some that contradict a brachyuran affinity, but it is known from a single specimen and the evidence is not definitive.[48,49] As with *E. praecursor* and *E. klugi*, the ventral morphology is poorly preserved. The original description reported chelate second pereopods,[50] which creates a contradiction. If *P. akaina* indeed has distal claws on the second pereopod, either a major character defining crown group Meiura[1] has evolved independently, or alternatively the species may fit well outside crown group Meiura.[48] Phylogenetic analyses (albeit with limited outgroup sampling) recovered *P. akaina* in either stem group anomuran or stem group meiuran positions.[2] Based on the information from each of the three important stem group taxa (Figure 4A), we hypothesize an uncarcinized ancestor for anomurans, though the ancestral state for crown group meiurans remains uncertain.

THE ECOLOGICAL ADVANTAGES OF BECOMING A CRAB ARE COMPLEX

The ecological breadth of crabs (living in nearly every aquatic habitat on Earth) departs from the view where convergent phenotypes are under positive selection in their particular habitats.[6,10,51] Scholtz[5] noted that carcinization, if viewed as the overall evolution of a broad, rounded shape from a more elongated one, is known from other arthropods such as horseshoe crabs (whose common name leads to mistaken identity: these are chelicerates, not crustaceans). None of the non-meiuran groups known, however, share the bent pleon. It is likely that carcinization in meiurans provides ecological advantages relative to uncarcinized sister taxa (e.g., mud shrimps, squat lobsters), allowing them to occupy new and varied niches. These may be broadly characterized as adaptations for protection, locomotion, and feeding.

The crab body plan may aid in protection and locomotion

The feature of carcinization most frequently discussed as adaptive is the reduced, folded pleon. In uncarcinized decapods (including squat

lobsters and hermit crabs; Figure 2G, I and Figure 2L–M, respectively), the elongated pleon is directly used for locomotion and predator avoidance, as in the behavioral caridoid escape reaction (i.e., tail-flip or backwards swimming).[13,52] Bending of the pleon in carcinization precludes the tail-flip behavior, but instead allows crabs to avoid predators by reducing the surface area exposed to attack. Calcification–the hardening of the pleonal cuticle usually observed in carcinization–further protects the animal from predators. The carcinized and calcified king crabs (Figures 1, 2N) evolved from within the shell-dwelling hermit crabs (Figures 2L–M, 3C). King crabs, and some partly carcinized hermit crabs including *B. latro*[14,53] (Box 1) have therefore abandoned their protective domiciles. The reasons are unclear, but may include moving into habitats where hiding under rocks may be favored over the additional expense of carrying the domicile,[23,54] or scenarios where gastropod shells were not available[22], forcing crabs to abandon their domiciles.

Carcinization may confer other advantages, such as improvements to locomotion. The bent pleon in combination with the flattened carapace allows a lower center of gravity than in uncarcinized decapods, freeing the posterior appendages for improved function,[49] particularly the sideways walking that typifies crabs. The sideways stance provides equally fast speeds when walking in either direction,[55] improving avoidance of forward attacking predators from merely hiding to an agile, active behavior. However, sideways walking is not observed in all carcinized lineages (e.g., forward-walking spider crabs and anomuran king crabs; Figure 5C and Figures 2N, 5B, respectively), and some uncarcinzed hermit crabs can walk sideways.[14,55,56] Improvements to mobility may also be characterized by reduced uropods associated with carcinization[25] (Figure 2), and specialized structures related to reproduction and pleonal positioning.[57–60] Therefore, it appears that a general posture of the pleon is the main requirement for locomotory benefits of carcinization, which can be achieved through various morphological pathways.

Decarcinization has occurred several times, despite the presumed loss of advantages from the exposed pleon and loss of sideways walking ability. Most decarcinized groups consist of singletons (Section 2.2) or groups with few extant species, such as the eubrachyuran family Corystidae and the porcelain crab genera *Euceramus* and *Porcellanella*. If all decarcinized groups were singletons or had very limited diversity, it could be hypothesized that decarcinization represents an evolutionary dead-end. Contradictory evidence comes from Raninoidea, or frog crabs (Figures 2C, 3F–G), a clade with low extant diversity (48 species) but also with > 200 fossil decarcinized members dating back to the Early Cretaceous.[40,61] Therefore, the crab-like body plan cannot represent an optimum for all niches, and may be subject to functional trade-offs that allow the evolution (and sometimes persistence) of decarcinization. Extant frog crabs inhabit sediments with few hiding places, and have adopted a fossorial lifestyle where rapid burying may protect the animal from predation,[40,62] but also concealing the animal as an ambush predator itself.[2] Perhaps the fossorial lifestyle exchanges lateral mobility for different protective benefits or larger body size,[63] a trade-off that may allow frog crabs to persist and diversify.[64] Future studies of functional morphology should explicitly
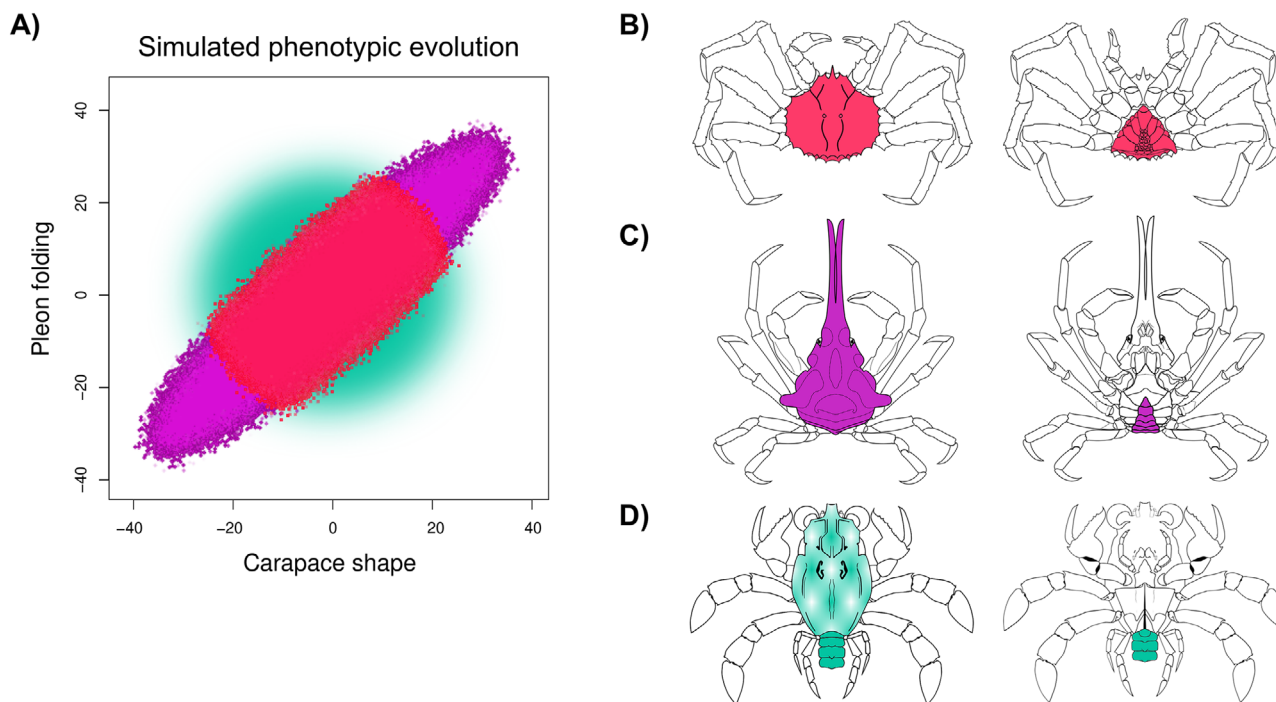
FIGURE 5 The crab-like body plan is an example of phenotypic integration. (A) Approximate areas of morphospace explored by simulations of phenotypic evolution, after [98,100]. Integrated structures (pink and violet points, representing the simulated covariance of carapace and pleon morphology) are constrained in the direction of variance due to their correlation. Modular, or non-integrated traits, will explore more directions of morphospace (cyan points) due to their lack of constraints. Over time, some taxa will achieve greater disparity in constrained directions (violet points) relative to those with modular traits, because the direction of selection is the same as the direction of constraint. (B) Example of integration between the dorsal carapace and pleon in a carcinized taxon (Lithodoidea: Lithodidae: *Paralithodes camtschaticus*). (C) Example of integration facilitating evolution of an extreme phenotype in a carcinized taxon (Eubrachyura: Majoidea: Epialtidae: *Oxypleurodon alisae*). (D) Example of decoupled evolution of the carapace (cyan gradient) and pleon (solid cyan) in a decarcinized taxon (Callichimaeroidea: Callichimaeridae: *Callichimaera perplexa*)

compare carcinized and non-carcinized taxa and their behaviors to better delineate benefits of the crab-like form.

Escalation of predation cannot explain early crab success

A feature of carcinization, observed mainly in eubrachyurans (Figures 2E–F, 3J) and some carcinized anomurans, is the development of laterally mobile claws.[14] When mineralized and adapted into forms that suit ecology, claws have been associated with the ability to crush prey and potentially with the diversification of the predatory crab groups. The evolution of crabs and their efficiency as shell-crushing predators, by adaptation of their claw morphology, has been implicated as a driver of an ecological arms race called the Mesozoic Marine Revolution. During this time, fauna such as molluscs and echinoderms evolved stronger and more heavily ornamented morphologies, possibly as a response to predation by decapod crustaceans.[65,66] Studies of prey taxa have focused on gastropods[67,68] and their fossils as a proxy recording defensive evolutionary trends towards the end of the Mesozoic.[65,69] Fossil crab claws that appear specialized for crushing hard-shelled prey (e.g., with asymmetrical claws, "molariform" pro-

trusions on the claw tips, and/or curved "teeth" on the proximal claw that aid in peeling open shells)[70] are first recorded from "mid" to Late Cretaceous deposits,[71–75] concurrent with the divergence[11] of eubrachyuran groups with known heavy shell predators such as xanthoids (Figure 2E) and portunoids during the so-called "Cretaceous Crab Revolution".[2]

Upon closer examination, however, the hypothesis of claw morphology and predation ability on hard-shelled invertebrates as a major influence on the evolutionary success of crabs and their carcinized body plans is overstated. Large claws can have other functions, including sexually selected weapons in fiddler crabs, which do not confer prey crushing ability but are crucial for signaling and antagonistic behaviors.[76,77] Therefore, some taxa bearing large, ornamented, and mineralized claws are not predators. The functional relationship between carcinized forms and shell-crushing is diluted by the presence of mineralized, asymmetrical, and ornamented claws and crushing mandibles in other decapods, such as lobsters,[5,70] and by varied crab diets including herbivory.[70,78–80] Of the carcinized anomurans, only porcelain crabs (Figures 2H, 3B) have a known Mesozoic fossil record.[11,81] Although porcelain crabs and *L. hirta* (Figure 2J) have broad claws, these taxa are mainly filter feeders, occasionally using their claws to scrape algae.[82] While some king crabs (Figures 1, 2N)

are indeed reported as shell-crushing predators with heavily calcified claws,[83,84] they appeared ~35 million years after the end of the Mesozoic.[4]

Overall, there is little relationship observed between gross claw morphology and function, and the timing or success of carcinization. While predation represents an effective ecological strategy for many groups of meiurans (and investigations into species of aquacultural interest may corroborate predatory behaviors[85]), it cannot be directly related to the evolution of body form or success of those clades.

THE CRAB BODY PLAN MAY REPRESENT A CASE OF PHENOTYPIC INTEGRATION BETWEEN THE PLEON AND CARAPACE

Repeated evolution of the crab body plan may entail phenotypic integration, that is, covariation among body parts[86] (Figure 5). Integration, usually attributed to functional or developmental relationships between the body parts, molds phenotypic evolution in various animal systems, such as correlation between the shapes of regions of vertebrate skulls, for example,[87–89] heads and mandibles in ants,[90] and appendage segments in mantis shrimp.[91] Above, we described possible ecological benefits for pleonal reduction in crabs, improving their ability to hide in narrow spaces and move faster. We hypothesize that carcinization broadly represents an example of morphological and functional integration, wherein the bent pleon has coevolved with the flattened and widened carapace, possibly emergent from functional improvements to predator avoidance and locomotion.

Certain carcinized features may predispose the emergence of others, such as the bent pleon necessitating reduction of pleonal muscles and fused pleonal ganglia.[13] In brachyurans, the evolution of specialized pleon holding structures correlates with carcinization,[57,59,60] while king crabs (Figures 1, 2N, 5B) calcified and folded the soft asymmetrical pleon of an ancestral hermit crab form (Figures 2L–M, 3C).[13] In most carcinized meiurans, the characteristic pleonal folding occurs fairly late in development, at the transition from planktonic megalopa stage to benthic juvenile forms.[19,92,93] Freshwater brachyurans exhibit extended brood care, which lack the metamorphic transition (the time when the pleon is moved under the body) and instead these taxa hatch immediately as relatively carcinized juveniles.[94–96] For decarcinized taxa with known development, the pleon is reduced but never folded, for example.[97] Perhaps decarcinized or partially carcinized taxa exhibit pedomorphosis,[2] wherein the carapace and pleon retain their relative positioning from larval stages (Figure 5D).

Traditionally, morphological integration has been viewed as a set of constraints that may limit the direction and magnitude of phenotypic evolution, with the alternative to integration being body parts that evolve as separate phenotypic modules that can diverge rapidly and therefore generate disparity.[98–100] While the relationship between carcinization and pleonal bending appears straightforward as described above, this is not the case for the carapaces of meiurans as they exhibit substantial morphological disparity. Figures 1–3 depict rel-

atively classical examples of dorsal morphology for carcinized, uncarcinized, and decarcinized taxa, but there are many exceptions within phenotypic categories (Box 1) as well as "extreme" morphologies, such as the teardrop shaped arrow crabs (the brachyuran *Stenorhynchus* and the squat lobster *Chirostylus*, not pictured) with legs more than twice the body length, or elbow crabs (Parthenopidae, not pictured) with triangular carapaces and elongated claws. A preliminary study of shape evolution has been conducted on meiuran dorsal carapaces, for five brachyurans and one king crab,[101] finding greater shape similarity between carapaces in four of the brachyurans and the king crab, and little between the majoid (spider or decorator crab; an example in Figure 5C) and other brachyurans. Extremes such as the spider crabs can break morphological expectations from both phylogeny (to resemble other, related eubrachyurans) and convergence (to look like other carcinized taxa). Therefore the crab body plan seems to contradict the traditional wisdom that integration constrains morphological disparity.

However, a growing number of recent studies have uncovered strong integration of body structures alongside and even facilitating high disparity.[88,102,103] In some clades, integrated body parts may explore fewer overall directions of morphospace than independent structures, but they can attain a great range of shapes within those phenotypic constraints[99,100] (Figure 5A–C). For crabs, it has been proposed that divergent carapace shapes may help taxa invade new communities or niches where local areas of morphospace are already occupied,[104] perhaps promoting carapace disparity. Integrated structures may also become decoupled into modules or partial modules,[87] sometimes due to a change in behavior or ecology,[105,106] complicating the observed correlations in morphospace. We hypothesize such decoupling has occurred in at least some decarcinized taxa (Figure 5D), where the carapace and pleon may never become integrated in juveniles or adults. Overall, phenotypic integration is a sensible macroevolutionary expression of convergent evolution,[98,106] and its pattern should be used to quantify carcinization.

TOWARDS PREDICTING THE EVOLUTION OF CRABS

From a mechanistic perspective, phenotype is the expressed result of genomic and transcriptomic regulation of development. Therefore, the constraints leading to convergent evolution of carcinization may share an underlying genomic signature. Such a proposal may seem counterintuitive given the morphological and functional differences between carcinized clades; however, deep homology of development often typifies the evolution of integrated structures.[98]

It is only within the last year that high-quality genomic resources have become available for meiurans, though only for carcinized members. Two species of eubrachyuran, *Portunus trituberculatus*,[107,108] and *Scylla paramamosain*[109] (both members of the same family), and one species of king crab, *Paralithodes platypus*[110] now have published chromosome-level genome assemblies. The eubrachyuran *Eriocheir japonica sinensis* also has a recently updated genome assembly.[111,112] To enable comparative research on whether genomic changes have a

relationship to the phenotypic changes defining carcinization, it will be essential to assemble further genome sequences, particularly for decarcinized and uncarcinized meiurans.

Currently, little is known about development of crustacean carapaces, or pleonal growth. Outgrowth of the dorsal carapace has been studied in the water flea *Daphnia magna* and in the amphipod *Parhyale hawaiensis*,[113] both of which are hundreds of millions of years diverged from decapods. Nonetheless, candidate genes from the gene regulatory network patterning the fly wing were expressed in the margin of the *D. magna* carapace,[113] suggesting that the dorsal carapace may share deep homology with proximal leg segments in other crustaceans, in addition to the insect wing.[114,115] Meanwhile, there are few obvious candidate genes for bending of the pleon in meiurans. Loci of interest could be identified by comparing transcriptomes across the metamorphic transition from megalopa larva to juvenile, when the pleon becomes folded in most crabs. One study[108] has implicated decreased expression in the *P. trituberculatus* transcriptome at exactly this stage for the *Hox* genes *Ubx* and *abd-A* (expression of the latter patterns the pleon in *P. hawaiensis*[116,117]). More is known about the genomics of metamorphosis in lobsters[118] and shrimp[119] than in meiurans. Therefore, it will be necessary to explore "novel" or taxon-restricted and non-coding loci that share more sequence or expression similarity based on degree of carcinization than on the species relationships. As phylogenetic relationships among meiruans move towards resolution (Section 2), comparative methods could be used to identify genomic targets, for example.[120,121] Such goals come with the caveat that convergent evolution may be predictable at some hierarchical levels of biological organization, but not at others, for example.[8,122]

CONCLUSIONS AND OUTLOOK

Convergent gains and losses of the crab-like body plan provide an excellent system for examining the predictability of phenotypic evolution and body form over macroevolutionary timescales. Understanding the ecological and genomic basis underlying convergence in body form will contribute to the importance of constraints across the tree of life.[6,123] Key priorities for future investigations should include: (1) phylogenomic sampling of poorly studied groups to better resolve the pattern of evolution of carcinization, (2) functional morphological research comparing anomurans and brachyurans to uncover the selective benefits of carcinization, (3) morphological comparisons interrogating the pattern of phenotypic integration and modularity in crabs, and (4) the assembly of genomes for exemplar carcinized and decarcinized taxa for comparative studies. Together, phylogenetic, morphological, and genomic evidence will reveal a comprehensive evolutionary scenario describing how to become a crab.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT
Data sharing not applicable to this article.

ORCID
Joanna M. Wolfe https://orcid.org/0000-0001-6708-8332
Javier Luque https://orcid.org/0000-0002-4391-5951

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